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Letter

Sex-Specific Differences in Thermal Fertility Limits

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Critical thermal limits (CTLs) are established viability thresholds when studying the impact of climate change on natural populations. Novel thermal fertility limits (TFLs) of species have been proposed alongside CTLs, to better assess the sublethal effects of rising temperatures on species persistence. However, sex-specific sensitivity of fertility to temperature also needs consideration.

Walsh *et al.* [1] highlighted the importance of monitoring and assessing fertility when investigating the impact of rising temperatures on natural populations. Models of the long-term impact of climate change on populations have focused on upper and lower critical thermal limits (CTLs) beyond which critical biological functions and specifically, survival, are compromised [2]. The authors noted that individual fertility is typically compromised at lower temperature thresholds than CTLs, whereupon individuals are viable but infertile, and this can therefore jeopardise population persistence. In their article, they propose a framework for examining species thermal fertility limits (TFLs) and the development of a standardised measure of fertility, similar to measures of viability and other standardised measures of CTLs [1]. An ecologically relevant limit to fertility, they add, is represented by the point (i.e., temperature threshold) at which an organism is unable to produce viable adult offspring under controlled conditions. The introduction of TFLs is timely and pivotal to correctly estimate the effects of sublethal temperatures on the persistence of natural populations. However, to properly frame TFLs for researchers new to fertility studies, it is important to highlight a crucial difference in the way male and female primary reproductive traits respond to thermal stress. In the species studied to date, the emerging pattern is that male gametogenesis appears more sensitive to thermal stress than female gametogenesis. These sex-specific differences in thermosensitivity can be observed in endothermic and ectothermic animals and also in plants (Table 1).

For example, in *Drosophila* spp., one of the better studied taxa, both in terms of sexual traits and the effects of thermal stress on reproduction, upper TFLs are reached at lower temperatures for males than for females [3]. *Drosophila buzzatii*, *Drosophila simulans*, and *Drosophila melanogaster* males, but not females, exposed to the same heat stress are infertile, as females mated to unexposed males produce viable offspring (reviewed in [3,4]). Similarly, within developing flowers of maize (*Zea mays*), tomato (*Lycopersicon esculentum),* and rice (*Oryza sativa)* (among others, reviewed in [5]), male reproductive organs appear more sensitive to temperatures $\geq$30°C than female reproductive organs. Reciprocal crosses between heat-stressed plants of those species revealed that the use of pollen produces significantly lower crop yield than when heat-stressed female plants are used as the receptor plant [5,6]. Temperature-induced male infertility arises, at least in insects and mammals, from impaired spermatocyte and spermatid form and elongation leading to abnormal sperm form and function and reduced sperm motility [3,7]. This is not to say that female reproductive organs are immune to heat stress. In mammals, heat stress affects spermatogenesis but also oocyte function, impairing fertilisation (reviewed in [7]). In the coral *Acropora digitifera*, an increase of 2°C in water temperature caused a significant decrease in sperm number and egg volume, but no change in egg number [8]. The underlying physiological and biochemical mechanisms for this male-biased sensitivity and, more generally, the mechanisms implicated in the dysregulation of male and female reproductive function, are unclear and in need of further study [3,5].

Accounting for these sex-specific differences in thermosensitivity is pivotal to model realistic scenarios for natural populations under heat stress. Female fertility, seemingly more resilient to heat-induced stress than male fertility, may buffer population persistence as temperatures continue to rise. This could happen via

Table 1. Examples of Sex-Specific Differences in Thermosensitivity on Fertility

Taxonomic group	Organism	Species	Measure	Sex affected	Refs
Insect	Fruit fly	Family: Drosophilidae	Offspring production, sperm motility	Males but not females	[3,10,11]
Vertebrate	Cow and bull	*Bos taurus*	Fertilisation	Both males and females	[7]
Poales	Barley	*Hordeum vulgare*	Gamete viability	Anthers but not ovules	[12]
Cnidarian	Coral	*Acropora digitifera*	Gamete number	Egg volume and sperm number but not egg number	[8]

dispersal, immigration, or be dependent on the level of mating promiscuity specific for that species or population. For example, polyandrous females may be able to reproduce where monoandrous females cannot. Moreover, the effects of male infertility might be compounded by the effects of heat stress on the likelihood of copulating [9]. In the design of quantitative point estimates of temperature limits for fertility that Walsh *et al.* [1] suggest to adopt, it will be important to consider that these estimates will likely vary between sexes (as well as depending on location, e.g., [10]). Equally, as TFLs can be defined as the temperature at which a determined proportion of individuals is sterile, at either an upper TF_{MAX} or lower TF_{MIN} thermal stress limits [1], it is necessary to emphasise that the proportion of infertile males and females at that point will differ. These sex-skewed differences on the proportion of infertile individuals will affect predictive models of distribution, abundance, and persistence of populations under different climate change scenarios. As we work towards producing standardised measures for TFLs, it is important to understand the functional mechanisms responsible for these sex-skewed differences in thermosensitivity on fertility. This will allow us to inform robust predictions on the effects of climate change on population stability and persistence, as well as to capitalise on any buffering properties of reproduction.

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